STATUS OF THE PEREGRINE FALCON *FALCO PEREGRINUS* ON LUNDY: BREEDING ECOLOGY AND PREY SPECTRUM

by

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ABSTRACT

Dense island sub-populations of Peregrine Falcons *Falco peregrinus* are common around the British Isles. Lundy offers a unique opportunity to study this specific area of Peregrine ecology. Manx Shearwaters *Puffinus puffinus* comprised a significant proportion of the prey spectrum; other important prey included: Herring Gulls *Larus argentatus*, Domestic Pigeons *Columba livia* and Rabbits *Oryctolagus cuniculus*. Preliminary data on breeding performance and nest cliff topography are presented. Further research is required to establish causality from the various limiting factors on the population; and inform how island populations of Peregrines are regulated in the United Kingdom.

Keywords: Peregrine Falcon, *Falco peregrinus*, Lundy, diet, breeding success

INTRODUCTION

Numerous offshore islands in the British Isles support dense sub-populations of Peregrine Falcons *Falco peregrinus*, often associated with seabird abundance (Ratcliffe, 1993). However, there appears to be no consistent pattern in current densities, with breeding pairs mainly absent from island groups such as St Kilda and the Shetland Islands, despite having relatively dense populations in the recent past (Ellis & Okill, 1993; Ratcliffe, 1993). Peregrines have been recorded as a breeding species on Lundy for over 750 years. They are the only regular breeding raptor, with historically up to two pairs resident on the island (Davis & Jones, 2007). In 2014, five breeding pairs were occupying nest territories on Lundy, one of the densest island breeding populations in the U.K. (Sutton, 2015a).

Understanding the dynamics of wild populations and predicting their behaviour requires knowledge of the method of population regulation (Hairston *et al.* 1960). Few studies have investigated the factors affecting high population density with island populations of Peregrines in the British Isles. As a small offshore island 18km from the nearest point on the mainland, Lundy offers the opportunity to study Peregrine population dynamics and predator-prey relationships in an area relatively free from direct human disturbance. This will give focus to understanding the ecological processes affecting the population and as an effective control to compare with other islands and sub-populations. Determining how Peregrine populations are regulated and what their
future prospects are requires an understanding of the various limiting factors on spatial and temporal scales.

The key objective of this study aims to identify the factors influencing Peregrine density on Lundy and then apply that knowledge to the management of this and other island populations. This could determine the various reasons why Peregrines are numerous on certain offshore islands and absent from others. Despite an increase of breeding Peregrines in urban and inland areas, coastal Peregrines in some traditional breeding areas are in decline (Balmer et al. 2013). Investigating the reasons for dense populations on islands such as Lundy could help to establish factors which may be influencing declines elsewhere in the U.K.

Therefore, the long-term goal of this research intends to (a) determine breeding performance from the various biotic and abiotic factors influencing productivity and (b) conduct a quantitative assessment of diet and establish any spatio-temporal variation in the prey spectrum. This paper is intended as a summary of the first two years' fieldwork and to present preliminary data on breeding ecology and dietary habits. This will set a foundation for future research and determine the various limiting factors on population density.

METHODS

Data collection
Observational data on breeding performance and nest cliff characteristics were collected during visits between April and July 2014-2015. A minimum of one visit per month was made to the island; either extended 3-4 day stays or day trips. Fieldwork was conducted by two surveyors checking sites independently. To ensure accuracy of observations from territories occupied at certain times, two-way radios were used to establish updates on activity at respective nest sites. Prey samples were collected between April and September 2013-2015. Samples were collected indirectly from prey remains left after feeding, and from direct observation of successful hunts, prey brought into a feeding perch or nest ledge and whilst observed feeding on prey.

Breeding performance
At least four visits are required to each individual nest territory during the Peregrine breeding season to monitor breeding performance (Hardey et al. 2009). Using the four visit schedule as a guide, the first visit was in early April to establish site occupation by territorial adult pairs. A second visit to confirm egg laying and incubation was carried out from early to late May. Young are expected to be visible on the ledge in June, when the third visits were conducted. To check for fledged juveniles a fourth visit was made to all territories in July.

To check for territory occupation, a systematic circuit was made of the island checking each territory in turn. All known and potential nest cliffs and ledges were observed with 10×42 binoculars and a 12×36 spotting scope. A nest territory was considered occupied if one or more adults were present and regular, fresh kills were observed in the immediate area of the nest territory (Hardey et al. 2009). No nest ledges were visited directly, though two were checked within <10m to confirm number and age
of pulli and breeding success. These checks were conducted with a Schedule 1 disturbance permit issued by the BTO on behalf of Natural England.

Where possible dates of first egg laying, hatching and fledging were recorded; as well as numbers of eggs, pulli and juveniles at each stage of the breeding cycle. It was not always possible to obtain data from nest ledges due to their position. At two of the breeding territories it was possible to infer the status of the nest from activity observed at the breeding cliff. These were behaviours such as incubation changeovers between adults, food deliveries to an incubating female or food brought to young on the nest ledge.

Nest cliff characteristics
Topographical data were recorded from each individual nest cliff where a breeding attempt was observed, whatever the outcome. Physical parameters from occupied nest cliffs where no breeding attempt was observed were not recorded. Nest cliff characteristics were determined using a handheld global positioning system (GPS) device to measure nest cliff and nest ledge height. A handheld base-plate compass was used to establish compass aspect of nest cliffs measured from the top of each cliff. These were defined as: North (N); North East (NE); East (E); South East (SE); South (S); South West (SW); West (W); North West (NW). Nest ledge type was recorded based on the substrate on which breeding pairs laid their clutch. Nest shelter was determined from the protection offered by each nest ledge as either: open; sheltered – one side; sheltered – two sides; overhang <45°; overhang >45°; recess (Mearns & Newton, 1988).

Diet and prey spectrum
Determining Peregrine food habits from prey remains is an established indirect method of assessing diet and foraging behaviour (Ratcliffe, 1993; Marti et al. 2007). Prey remains were recorded on a circuit of the island whilst checking breeding territories. This is similar to a method conducted by Velarde (1993) to assess Peregrine diet on an island in the Gulf of California. Systematic searches were conducted within territories, checking regular plucking areas and slopes adjacent to nest cliffs. Remains including feathers, bones and carcasses were found, either plucked or consumed on the island’s paths or on feeding areas within nest territories. Recording prey from nest ledges was possible at one site dependent on breeding success. However, collections from other nest ledges were restricted due to access and logistics of organising climbers.

Prey remains that were accessible were removed from their location into sample bags and recorded with a ten-figure Ordnance Survey grid reference to prevent the possibility of recording samples twice on a subsequent visit. Where prey remains were observed on inaccessible feeding areas, a Digital Single Lens Reflex (DSLR) camera fitted with a 500mm telephoto lens was used to record an image for later analysis. Identification was determined from field samples to those in reference books (Brown et al. 2003) and from personal experience (Sutton, 2015b). Where identification of a prey species was unknown, samples were sent to E. Drewitt, a Peregrine researcher with extensive experience in identifying prey species (Drewitt & Dixon, 2008). To avoid duplication of prey frequency, the number of individuals counted was assessed by checking for the same wing feathers or other body parts.
Prey remains of Peregrines are easily identified; on carcasses the breast is usually ruptured and totally consumed and the breastbone often has distinct notches made from the Peregrines powerful beak when feeding (Bang & Dahlstrom, 2011). Plucked feathers will often be found close by and on smaller prey there may be no carcass but a small, neat pile of feathers indicating a kill. Other potential predators of birds such as Great Black-backed Gulls *Larus marinus* do not have the hooked beak of a raptor to pluck their prey and tend to consume prey whole. In particular when feeding on shearwaters, the skins are distinctly turned inside out (Corkhill, 1972), as opposed to Peregrine feeding remains described above.

**Statistical analysis**

Prey items were divided into nine prey groups (ducks/waders, shearwaters, auks, gulls, pigeons/doves, corvids, small passerines, lagomorphs, other) and five weight classes (<50g; 51-250g; 251-500g; 501-1000g; >1000g). Variation in total prey frequency and prey weight classes between 2014 and 2015 was compared using the *G*-test (Fowler & Cohen, 1996; Dytham, 2011). Pearson’s product moment correlation coefficient (*r*) was used to test the relationship between prey weight and frequency of predation. Fisher’s Exact test was used to compare the frequency of Herring Gull *Larus argentatus* predation between 2014 and 2015. Statistical calculations were performed using Minitab 17© computer software and Excel© spreadsheets provided by McDonald (2014).

**RESULTS**

**Breeding performance**

In 2014 there were five territorial adult pairs and a single female occupying nest territories on Lundy. Three adult pairs were occupying territories on the East Side, one adult pair on the South End and one adult pair and a single adult on the West Side. There were no pairs present in the North West quarter of the island. Based on the number of territories occupied by adult pairs, productivity (number of young fledged per occupied pair) was 0.20 (*n*=5). Breeding success (number of young fledged per successful pair) was 1.00 (*n*=1). Only one pair bred successfully, fledging a single female from a two egg clutch. Two pairs attempted to breed but failed at the egg or nestling stage and no evidence of breeding activity was observed with the remaining two territorial pairs. An adult female was observed occupying a known territory throughout the breeding season, but with no evidence of an adult male in residence (Table 1).

In 2015 there were five territorial adult pairs occupying nest territories and one adult present at a territory in April. Two adult pairs were occupying territories on the East Side, one adult pair on the South End and two adult pairs on the West Side. A single adult was observed displaying territorial behaviour on three occasions at a nest cliff in April on the East Side but was not seen subsequently during the breeding season. There were no pairs present in the North West quarter of the island. Productivity in 2015 was 1.00 (*n*=5), significantly higher than in 2014 with two pairs on the east side fledging a total of five juveniles. Breeding success was 2.50 (*n*=2). There were no observed breeding attempts at the remaining three territories (Table 2).
The distribution of breeding pairs and occupation of territories varied between the two years (Tables 1 and 2). In 2014 the mean distance between nest cliffs was 1.24km (SD ±0.51, range 0.75-1.70, n=5). In 2015 the mean distance between nest cliffs was 1.60km (SD ±0.66, range 0.84-2.45, n=5), measured from the North North East (NNE) territory in a clockwise linear direction heading south. Based on a total land area of 445ha, the mean number of hectares per adult pair in both 2014 and 2015 was 89ha.

**Nest cliff characteristics**

The mean height of breeding cliffs was 70.40 metres above sea level (m/asl) (SD ±22.50, range 47-108, n=5). The mean height of nest ledges was 53.80m/asl (SD ±10.01, range 37-64, n=5). Nest cliffs used for breeding attempts faced between South and East and the substrate for every breeding attempt was on bare soil, except at territory L1/NNE where a disused Raven *Corvus corax* nest was used. Nest shelter varied between breeding ledges; nests were either open to the weather or had some form of protection from an overhang (Tables 3 and 4).

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**Table 1**: Territory occupation and breeding success of Peregrine Falcons *Falco peregrinus* on Lundy 2014

<table>
<thead>
<tr>
<th>Territory</th>
<th>Occupancy</th>
<th>Eggs</th>
<th>Pulli</th>
<th>Fledged</th>
<th>Other Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1/NNE</td>
<td>Pair</td>
<td>≥ 1</td>
<td>0</td>
<td>*</td>
<td>Failed breeding attempt</td>
</tr>
<tr>
<td>L2/NE</td>
<td>Vacant</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>No adults present</td>
</tr>
<tr>
<td>L3/E</td>
<td>Pair</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>Single female fledged</td>
</tr>
<tr>
<td>L4/SE</td>
<td>Pair</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>No breeding attempt observed</td>
</tr>
<tr>
<td>L5/S</td>
<td>Pair</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>No breeding attempt observed</td>
</tr>
<tr>
<td>L6/SW</td>
<td>Pair</td>
<td>≥ 1</td>
<td>0</td>
<td>*</td>
<td>Failed breeding attempt</td>
</tr>
<tr>
<td>L7/W</td>
<td>Single</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>Adult female present all year</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>≥ 4</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

**Table 2**: Territory occupation and breeding success of Peregrine Falcons *Falco peregrinus* on Lundy 2015

<table>
<thead>
<tr>
<th>Territory</th>
<th>Occupancy</th>
<th>Eggs</th>
<th>Pulli</th>
<th>Fledged</th>
<th>Other Information</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1/NNE</td>
<td>Pair</td>
<td>≥ 2</td>
<td>≥ 2</td>
<td>2</td>
<td>One male and one female fledged</td>
</tr>
<tr>
<td>L2/NE</td>
<td>Single</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>Adult present in April</td>
</tr>
<tr>
<td>L3/E</td>
<td>Pair</td>
<td>≥ 3</td>
<td>3</td>
<td>3</td>
<td>Two males and one female fledged</td>
</tr>
<tr>
<td>L4/SE</td>
<td>Vacant</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>No adults present</td>
</tr>
<tr>
<td>L5/S</td>
<td>Pair</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>No breeding attempt observed</td>
</tr>
<tr>
<td>L6/SW</td>
<td>Pair</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>No breeding attempt observed</td>
</tr>
<tr>
<td>L7/W</td>
<td>Pair</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>No breeding attempt observed</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>≥ 5</td>
<td>≥ 5</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>
Prey spectrum

In total, 275 prey samples were collected and recorded to a specific species or genus. A total of 26 species are represented within this sample, comprising 25 bird and one mammal species (Rabbit *Oryctolagus cuniculus*). Bird species ranged in size from Common Chiffchaff *Phylloscopus collybita*, mean weight of adults eight grams, up to Mallard *Anas platyrhynchos*, mean weight of adults 1210g (BTO, 2015).

The most common prey species were Manx Shearwaters *Puffinus puffinus* by frequency (41.81%) and biomass (33.27%). Other significant prey species (>5 by total frequency and >10 kg by total biomass) are given in Tables 5 and 6. The most common prey group were shearwaters (comprised wholly of Manx Shearwater) by both frequency and biomass. Other prey groups by frequency and biomass are given in Figure 1.

Herring Gulls were the second most common prey species by frequency (12.72%) and biomass (25.38%) (Tables 5 and 6). Of the 35 individuals recorded, 80.00% were immature and 20.00% adults. There was no significant difference in frequency of predation between 2014 and 2015 (Fisher’s Exact, *P*=0.672). The rate of predation on adults and immatures was similar in both years (Table 7).

### Table 3: Nest site characteristics of Peregrine Falcon *Falco peregrinus* breeding cliffs on Lundy 2014

<table>
<thead>
<tr>
<th>Territory</th>
<th>m/ast</th>
<th>Aspect</th>
<th>m/ast</th>
<th>Type</th>
<th>Open</th>
<th>One side</th>
<th>Two sides</th>
<th>NS</th>
<th>TD</th>
<th>Recess</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1/NNE</td>
<td>66</td>
<td>South East</td>
<td>56</td>
<td>Stick nest</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L2/NE</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L3/E</td>
<td>47</td>
<td>East</td>
<td>37</td>
<td>Bare soil</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L4/SE</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L5/S</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L6/SW</td>
<td>108</td>
<td>South</td>
<td>64</td>
<td>Bare soil</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L7/W</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

● - Successful breeding attempt; ○ - Failed breeding attempt

### Table 4: Nest site characteristics of Peregrine Falcon *Falco peregrinus* breeding cliffs on Lundy 2015

<table>
<thead>
<tr>
<th>Territory</th>
<th>m/ast</th>
<th>Aspect</th>
<th>m/ast</th>
<th>Type</th>
<th>Open</th>
<th>One side</th>
<th>Two sides</th>
<th>NS</th>
<th>TD</th>
<th>Recess</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1/NNE</td>
<td>66</td>
<td>South East</td>
<td>56</td>
<td>Stick nest</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L2/NE</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L3/E</td>
<td>65</td>
<td>East</td>
<td>37</td>
<td>Bare soil</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L4/SE</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L5/S</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>L6/SW</td>
<td>108</td>
<td>South</td>
<td>64</td>
<td>Bare soil</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
<td>●</td>
</tr>
<tr>
<td>L7/W</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

● - Successful breeding attempt
Rabbits were important in terms of biomass (19.34%) and to a lesser extent frequency (5.81%) (Tables 5 and 6; Figure 1). They were recorded as prey in all months except August, with a peak in June and July (62.50% of total Lagomorphs by frequency); and at four Peregrine territories (L1/NNE; L3/E; L4/SE; L6/SW), with the pair at territory L3/E taking 43.75% of total Lagomorphs by frequency.

Prey in the 250-500g weight class were taken most frequently ($n=157$), followed by prey in the 500-1000g weight class ($n=50$). There was a very weak positive relationship between prey weights and frequency of predation ($r=0.140$, df=31, $P=0.451$). The majority of prey taken (75.63%) were <500g in weight (Figure 2).

There was a statistically highly significant difference in the nine prey groups ($G=15.703$, df=5, $P=0.007$) and a significant difference in the five prey weight classes ($G=10.256$, df=4, $P=0.036$) between the years 2014 and 2015. There is strong evidence for variation in prey frequency by prey group and weight between the two years (Figures 3 and 4).

### Table 5: Prey species (>5 by total frequency) taken by Peregrine Falcons *Falco peregrinus* breeding on Lundy 2013-2015

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Frequency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manx Shearwater <em>Puffinus puffinus</em></td>
<td>115 (41.81)</td>
</tr>
<tr>
<td>European Herring Gull <em>Larus argentatus</em></td>
<td>35 (12.72)</td>
</tr>
<tr>
<td>Domestic Pigeon <em>Columba livia</em></td>
<td>29 (10.54)</td>
</tr>
<tr>
<td>Rabbit <em>Oryctolagus cuniculus</em></td>
<td>16 (5.81)</td>
</tr>
<tr>
<td>Eurasian Skylark <em>Alauda arvensis</em></td>
<td>10 (3.63)</td>
</tr>
<tr>
<td>Meadow Pipit <em>Anthus pratensis</em></td>
<td>9 (3.27)</td>
</tr>
<tr>
<td>Black-legged Kittiwake <em>Rissa tridactyla</em></td>
<td>6 (2.19)</td>
</tr>
</tbody>
</table>

### Table 6: Prey species (>10 kg by total biomass) taken by Peregrine Falcons *Falco peregrinus* breeding on Lundy 2013-2015. Average weights taken from BTO (2015) and ¹Mammal Society (2015); all measurements of mass in g.

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Biomass (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manx Shearwater <em>Puffinus puffinus</em></td>
<td>44045 (33.27)</td>
</tr>
<tr>
<td>European Herring Gull <em>Larus argentatus</em></td>
<td>33593 (25.38)</td>
</tr>
<tr>
<td>Rabbit <em>Oryctolagus cuniculus</em>¹</td>
<td>25600 (19.34)</td>
</tr>
<tr>
<td>Domestic Pigeon <em>Columba livia</em></td>
<td>10400 (7.89)</td>
</tr>
</tbody>
</table>

### Table 7: Predation rate by frequency on Herring Gulls *Larus argentatus* by Peregrine Falcons *Falco peregrinus* on Lundy 2014-2015. All figures in brackets are (%)

<table>
<thead>
<tr>
<th>Herring Gull</th>
<th>2014</th>
<th>2015</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>2 (13.30)</td>
<td>5 (25.00)</td>
<td>7 (20.00)</td>
</tr>
<tr>
<td>Immature</td>
<td>13 (86.70)</td>
<td>15 (75.00)</td>
<td>28 (80.00)</td>
</tr>
<tr>
<td>Total</td>
<td>15</td>
<td>20</td>
<td>35</td>
</tr>
</tbody>
</table>
Figure 1: Prey groups by total frequency and biomass (%) taken by Peregrine Falcons *Falco peregrinus* breeding on Lundy 2013-2015. Average weights taken from BTO (2015) and ¹Mammal Society (2015); all measurements of mass in g. ²Prey group ‘Other’ consists of Common Cuckoo *Cuculus canorus*

Figure 2: Predation frequency by weight of individual prey species taken by Peregrine Falcons on Lundy 2013-2015. Average weights taken from BTO (2015) and Mammal Society (2015); all measurements of mass in g.

Figure 3: Variation in frequency of prey groups taken by Peregrine Falcons *Falco peregrinus* breeding on Lundy between 2014-2015. (Note: Prey group *Auks* merged with *Ducks/Waders*, prey group *Corvids* merged with *Small passerines* and prey group *Other* removed to perform statistical tests)
DISCUSSION

The results presented here show that breeding productivity of Peregrines on Lundy can vary significantly between years. Nest site characteristics varied between territories with no obvious link to breeding performance. However, nest cliff aspect may be an important factor in breeding success, linked to climatic conditions. Therefore, long-term data sets are required to establish causal links to the various limiting factors on the population. Continued data collection on productivity, nest site quality, food supply and weather is required to establish causality.

Peregrines on Lundy have a varied diet, with Manx Shearwaters being the principal prey. This was expected from such a marine location, though the finding that Herring Gulls, in particular immatures, are an important food source was unexpected. Another unexpected result was the importance of Rabbits in the prey spectrum. The results suggest a significant difference in the frequency of prey groups and prey weights between 2014 and 2015. This is possibly related to an increase in demand for food from a more productive breeding year in 2015 than 2014.

The ability to access feeding areas to find prey remains at coastal Peregrine territories is restricted by topography and weather. Indirect methods may over-represent larger or brightly coloured prey species compared to smaller or darker prey remains that could go undetected (Ratcliffe 1993). Not all plucking points were known or accessible. Prey was observed being brought into nest ledges or feeding areas at territories L1/NNE and L3/E that were inaccessible and out of sight (pers. obs.). Loss of remains due to weather and scavenging may also bias the results (Drewitt & Dixon 2008).

Direct observations accounted for a small percentage of the total prey samples but were included to prevent any bias towards larger and more noticeable prey species. On 13 April 2015, the resident pair at territory L5/S were observed hunting migrant passerines over the South Light. They were seen to make >15 hunts, with six successful. However, they consumed their prey whilst flying, except for one which was taken to a plucking perch (S. Loram, pers. comm.). This shows that it is feasible that prey groups...
such as small passerines could be under-recorded depending on the method of data collection. It follows that the prey species results presented here are only representative of what prey remains were observed and accessible.

**Breeding performance**

Breeding densities of Peregrines from numerous studies show relative stability over long periods of time (Newton, 1979). The sub-population on Lundy has followed this trend with between five to six pairs occupying nest territories from 2002 to 2014 (Sutton, 2015a). Breeding success varied significantly between 2014 and 2015 (0.20 and 1.00) but it would be difficult to establish any reasons for this difference with such a small sample size. The figure for 2015 (1.00) is at the lowest end of the normal range given by Newton (1987). A long-term data set is required to observe any trends and possible links to food supply, weather and nest site quality.

With such an abundance of prey in the form of seabirds on Lundy, food supply may not be significant. However, productivity can vary markedly in cold or wet regions, such as western Britain, with variations in weather affecting breeding success. This is mainly through prey availability and hunting efficiency, as well as direct mortality from extremes of weather (Newton, 1979). Breeding success of Peregrines on the Aleutian Islands varied annually relative to spring climatic conditions. During rough weather, their main prey of auks remained far offshore making them harder to catch. Subsequently, fewer Peregrines nested and clutch desertions were more common (White, 1973).

**Nest cliff characteristics**

Breeding cliff height and nest ledge exposure have been shown to be strongly linked to breeding success in Peregrines (Mearns & Newton, 1988). This is related to greater hunting success from higher cliffs from which to locate and catch prey and reduced exposure at the nest to weather conditions. From the limited data here, it is interesting to note that the only breeding pair successful in both years was on the East Side (Territory L3/E). The nest cliffs used by this pair faced East and yet were the lowest in height and the nest ledges were the most exposed and at the lowest height.

The anomaly in nest cliff height may be explained by the presence of several large buttresses on the slope above the nest cliff, which the adults use to perch hunt from (pers. obs.). Three regular hunting perches on one of these buttresses are at heights of 120, 108 and 103m/asl. This may enable the adults to locate and catch prey more efficiently from a high vantage point, thus saving energy. Jenkins (2000) found that high hunting perches on nest cliffs or in nest territories contributed to increased foraging success by providing a distinct height advantage over their prey.

The two pairs in 2014 that attempted but failed to breed successfully both used nest ledges with some form of protection from the weather (Table 3). This suggests there are other limiting factors present, either working alone or in combination that restrict the ability of breeding pairs to reproduce successfully. Nest cliff aspect or location on Lundy therefore may be important; territories on the East Side or nest cliffs facing East will be considerably more protected from the prevailing weather. This then allows these breeding pairs to use less sheltered nest ledges on lower cliffs.
Prey spectrum

Manx Shearwaters

The presence of high densities of breeding Peregrines on offshore islands has been linked to large numbers of breeding seabirds resident in the same area (Nelson & Myres, 1976). Early results from this study show the importance of Manx Shearwaters in the diet of Peregrines breeding on Lundy. They were the most common prey species and prey group by both frequency and biomass (Tables 5 and 6; Figure 1). There was also a significant difference in the number of Manx Shearwaters taken between a poor breeding year (2014) and a good breeding year (2015) (Figure 3). This suggests a possible numerical as well as a functional response in the resident Peregrines to the increase in the number of Manx Shearwaters breeding on Lundy.

From 2003 to 2013, the breeding population of Manx Shearwaters on Lundy increased ten-fold to an estimated 3,451 pairs (Booker & Price, 2014). Considering the Peregrine breeding population has remained between 5-6 pairs from 2002 to 2014 (Sutton, 2015a), and assuming the same level of predation on shearwaters, it is unlikely that predation by Peregrines restricts the number of breeding Manx Shearwaters on Lundy. Further evidence for this is also suggested by the level of productivity in breeding Manx Shearwaters on Lundy, which is similar to other rat-free colonies (Booker & Price, 2014). Several of these other island colonies have similar densities of breeding Peregrines, as well as other predators of shearwaters such as Great Black-backed Gulls. It is possible that Peregrines and other predators are taking a high proportion of surplus non-breeding shearwaters, therefore having little effect on the breeding population (Newton, 2013).

Herring Gulls

Predation of Herring Gulls has been recorded previously in other dietary studies of coastal Peregrines (Ratcliffe, 1993; Sutton, 2015b). However, they are more commonly killed or injured in territorial disputes and considered too large and powerful to be taken as prey (Drewitt, 2014). The frequency of predation given here on both immatures and adults is unprecedented (Table 7). They were the second most common prey species by frequency and biomass (Tables 5 and 6). Interestingly, the total rate of predation was similar in both 2014 and 2015 (Table 7), suggesting that the taking of these large prey species had little effect on Peregrine breeding productivity. This is contrary to Dawson et al (2011), who found that Peregrines that predate larger prey consequently have increased breeding success. The majority taken were on the West Side and Pondsbury area in between Peregrine territories L6/SW and L7/W. This is also the area where the majority of the breeding population of Herring Gulls on Lundy resides (Davis & Jones, 2007). Both these Peregrine territories failed to produce young in either year, which suggests a functional rather than a numerical response to predation of Herring Gulls. Given the number of immature gulls taken (80%), prey vulnerability may also be an important factor (Quinn & Cresswell, 2004). Young Herring Gulls may not have the awareness, speed or strength to evade capture by Peregrines on Lundy.

Rabbits

Peregrines are known to take mammalian prey in the British Isles, in particular lagomorphs such as rabbits, though this is infrequent (Ratcliffe, 1993). Though Gilbert
(1927) states some coastal pairs in Pembrokeshire fed largely on small rabbits. Court et al. (1988) found that tundra Peregrines breeding in Arctic Canada regularly predate mammals. Three species, Arctic Ground Squirrels *Spermophilus parryii*, Collared Lemmings *Dicrostonyx groenlandicus* and Brown Lemmings *Lemmus sibiricus* were recorded as prey at 25-50% of nests. This was during a population peak of these mammals, which coincided with increased reproductive success in the local Peregrine population. Court et al. suggested that there was a correlation between these two events and that the resident Peregrines responded numerically to the seasonal abundance of mammals. Bradley & Oliphant (1991) provide further evidence for this behaviour in a non-peak year of mammal abundance: both lemmings and ground squirrels comprised a significant proportion of diet by frequency (29%) and biomass (33%). They also suggest that lack of tree cover on the tundra facilitates the capture of mammals. Considering the tree-less tundra-like landscape on Lundy, this may also apply to Peregrines breeding on the island.

The rate of predation by Peregrines on rabbits was similar in both 2014 and 2015 (Figure 3), suggesting that there was no numerical response to this behaviour in Peregrine breeding performance. However, the majority were taken during June and July at peak demand for food from nestlings, and at territory L3/E which was the most successful breeding site over the two years (see Results; Tables 1 and 2). Therefore, there could be a numerical response but with such a small sample size any assumptions must be treated with caution. The rabbit population on Lundy currently stands at approximately 1000 (Davis & Jones, 2014) but has fluctuated considerably, related to outbreaks of disease. As no consistent trend is available for rabbit population size and distribution, further research on this species is required to assess its impact as a prey species on Peregrine breeding performance and density.

**CONCLUSIONS**

Determining the various limiting factors on the regulation of populations is complex, and often the synthesis of multiple variables (Newton, 2013). It is likely that Peregrine abundance and productivity on Lundy is influenced by a combination of both density-dependent and density-independent factors. These may vary on spatial and temporal scales, according to certain environmental conditions. Therefore, continued research on this population is required to produce long-term data sets from which specific trends can be established.

Understanding whether the number and distribution of the Manx Shearwater population on Lundy directly affects Peregrine breeding success is a key question to be determined from future research. The results given here show that more shearwaters are taken when food demand is high from successful broods. Though there is no evidence that Peregrine density has increased in line with the Manx Shearwater population, the abundant food supply, in the form of shearwaters, could facilitate an increase in productivity in the Peregrine population. Determining trophic relationships and relating those results to population dynamics in both predator and prey species is essential. This may establish how populations of birds are regulated on islands such as Lundy.
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